Reference: *Biol. Bull.,* **155**: 576–585. (December, 1978)

VISUAL BEHAVIOR, EYE AND RETINA OF THE PARASITIC FISH *CARAPUS MOURLANI*

V. B. MEYER-ROCHOW AND M. K. TIANG

Department of Biological Sciences, University of Waikato, Hamilton, New Zealand

During the 1975 "Alpha Helix" South East Asia Bioluminescence Expedition to the South Moluccan Islands, three species of carapid fishes (*Carapus homei, C. parvipinnis,* and *C. mourlani:* Meyer-Rochow, 1977) were caught. All three inhabit various sea-cucumbers or large starfish of the genus *Culcita.* For many species it is still unknown how often and whether they leave their host at all for feeding, but there is now, at least for *C. mourlani,* some evidence that this species is a parasite which not only obtains shelter from its host but also devours its gonads and gut diverticula (Jangoux, 1974).

A report by Mortensen in 1923 indicated that carapids must be very abundant in the South Moluccas, but no specimens were taken during the 1973 Rumphius Expedition I (Springer, Burhanuddin and Gomon, 1974). Presumably because of their nocturnal and cryptic behavior these fishes often remain unnoticed (*e.g.,* local Banda fishermen were apparently unaware of the occurrence of fish inside starfish and often watched with great curiosity when we opened a *Culcita* during the "Alpha Helix" expedition). The rate of infestation of *Culcita* by *C. mourlani* is remarkably high: Mortensen (1923) found every second starfish infested, and Meyer-Rochow (1977) reports a slightly lower value of 1 fish per 2.1 starfish.

The behavior of these unusual fishes, which are popularly known as inquiline or intestine fish, pearlfish or assfish, has attracted the attention of natural historians (Emery, 1880; Arnold, 1953; Trott, 1970), ichthyologists (Smith, 1955; Arnold, 1956; Trott, 1970) and physiologists (Seymour and McCosker, 1974) for a long time. Greenwood, Rosen, Weitzman and Myers (1966) suggest that on the basis of morphological and ecological factors, pearlfishes form one of three families of the sub-order Ophidoidei, which are placed with the gadiform fishes. Courtenay and McKittrick (1970), after comparing sound-producing mechanisms in these fishes, come to the same conclusion and confirm the close affinities between carapids and ophidiids.

To the best of the author's knowledge the eye and retinal organization of a carapid fish have never before been studied in detail, although the adult eye (Nicol, Zyznar, Thurston and Wang, 1975) and larval eye (Meyer-Rochow, 1972) of related ophidiids have been examined. However, on the question of whether carapids use their photoreceptors at all, some information is available. Trott (1970) in *Jordanicus gracilis* and Meyer-Rochow in *C. mourlani* (this paper) have observed that these two species exhibit pupillary contraction after exposure to bright light. Pupillary reflexes among fishes are rare and seem confined to primarily crepuscular or nocturnal species (*e.g.,* eel). Although a carapid fish seems to employ olfaction and touch in locating the entrance to its host, be it anus (in case of holothurian) or mouth (in case of the starfish), vision, too, plays a part.

It can easily be demonstrated that a fish which is isolated from its host prefers a dark place and swims to the darkest corner of the aquarium. The fish also follows the starfish when the latter is moved about behind a glass division. *C. mourlani* also swims into a hollow human fist, when a little entrance large enough to allow the fish's passage, is left. These observations, which were carried out on freshly caught animals in aquariums on Groot Banda, clearly indicate that vision, in spite of the thick outer skin which covers the eyes of *C. mourlani,* cannot be totally useless to this species. In order to find out how the animal uses its photoreceptors, the eye and structural organization of the retina had to be investigated.

Materials and Methods

During the 1975 "Alpha Helix" South East Asia Bioluminescence Expedition the eyes of five *Carapus mourlani* were prepared for this study. The fish were recovered from the coelomic cavity of large cushion starfish (*Culcita novaeguinaea*), which were collected by free-diving in shallow water between Goenung Api and Groot Banda (Banda Islands, Indonesia).

The eyes were prefixed for 12 hr in 3% sea water/0.2 M cacodylate-buffered glutaraldehyde, washed several times in a mixture of 50 ml filtered sea water, 20 ml Na Cl, 10 ml 0.2 M Na-cacodylate and 0.05 ml $CaCl_2$, and postfixed for 2 hr in 1% OsO_4. The specimens were then dehydrated in a graded series of acetone, embedded in Spurr's epoxy resin and hardened for 2 days at 65° C.

Reichert ultramicrotomes were used to cut sections for both light microscopy (stained with toluidine-blue for approximately 1 min) and transmission electron microscopy. The ultrathin sections were double-stained with uranyl acetate (20 min) and lead citrate (3 min) and observed with either a Philips 200 or a Philips 300 electron microscope.

Results

General morphology

In a 160 mm (total length) specimen of *C. mourlani* the eye is slightly oval in shape with an anterior/posterior long axis of 4.2 mm and a dorso ventral shorter axis of 3.6 mm (Fig. 1). The eye appears to grow in proportion to increased total body length, but epidermal cell layers, due to their increasing thickness and opacity, must impair vision more severely in aged specimens. The pupil in a light-adapted specimen measures approximately 0.5 mm in diameter, but can dilate to at least 2.5 times this value in complete darkness. The iris in a fresh, living specimen is of an attractive gold-metallic color. Eyeshine in dark-adapted eyes was not observed. If it occurs at all, it must be very weak and of short duration.

As in other fishes, the orbit, which in a 160 mm specimen measures approximately 5 mm in diameter, is surrounded by orbito/temporal skull bones (Fig. 2), of which alisphenoid and orbitosphenoid form the inner wall. On the outside the orbit is surrounded by supraorbitale, dermosphenoticum and other dermal infraorbitalia, all of which are of surprisingly firm consistency. This may be interpreted as an adaptation to the pressures that this region of the head has to withstand

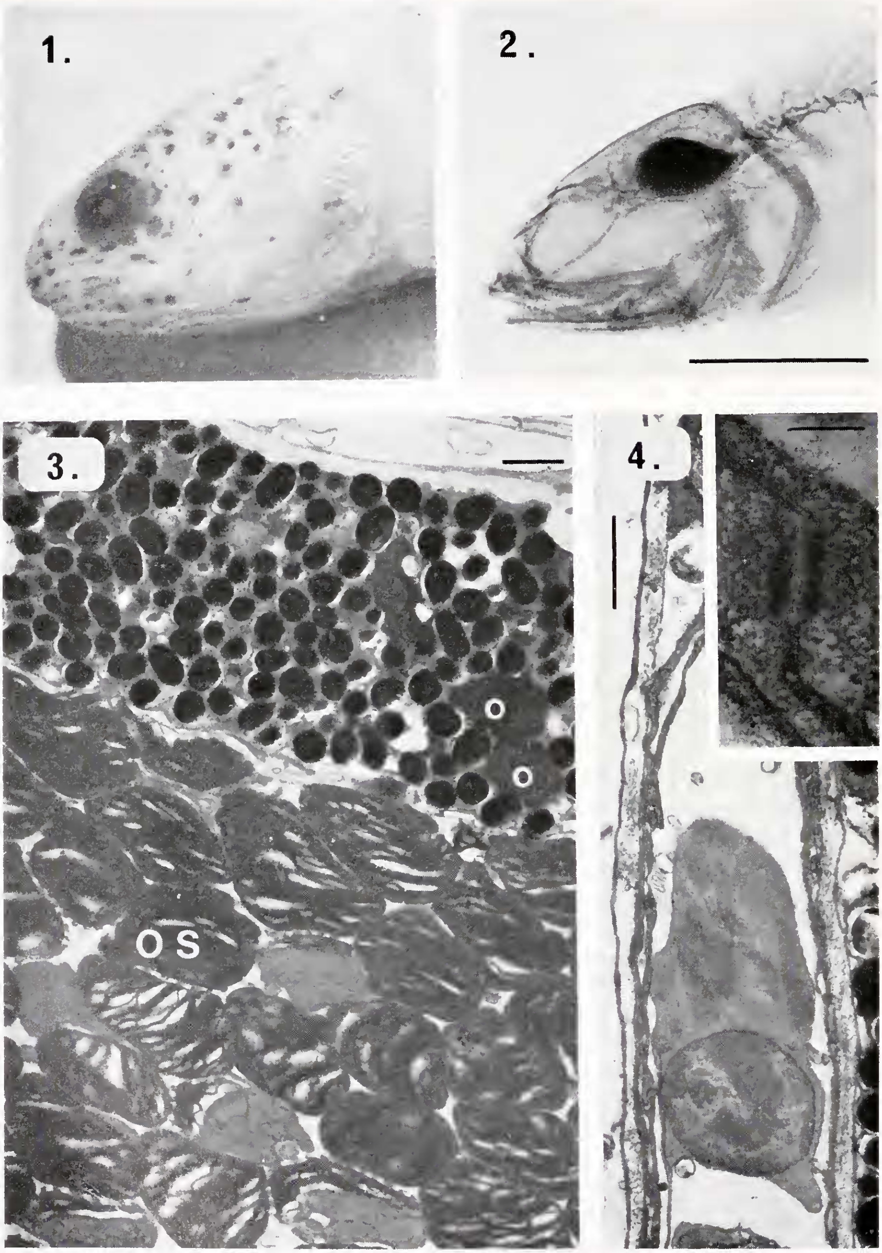


FIGURE 1. Close-up photograph of the head of a 160 mm (total length) *Carapus mourlani*. Apart from a few scattered melanophores, the fish is pale. The eyes lie under a relatively thick layer of cream-colored, semi-transparent skin.

FIGURE 2. Otoliths, skull bones as well as the orbital space show up clearly in this X-ray photograph. The scale, which is also applicable to Figure 1, is 1 cm.

when the animal penetrates anal or oral openings of holothurian and starfish, respectively.

The lens is spherical and has a diameter of 0.7 mm in a 80 mm individual. It consists of long, densely-packed living cells. The distance between retina and lens center is, on average, two times the lens radius. The choroid rete mirabile is inconspicuous and presumably reduced, as in deep-sea forms (for more detailed information on the question of blood supply to the eye of fishes see publications by Wittenberg and Haedrich, 1974, and Copeland and Brown, 1976).

The retina and associated structures

Capillaries. The retina is well-supplied with capillaries. Capillaries of varying diameter can be see within the retina and on the inner surface of the retina as well. Blood cells and their nuclei are often discernable in sections of retinal capillaries (Fig. 4). Fish eyes do not have, in general, the massive network of capillaries seen in the mammalian eye. However, from the work of Ali, Anctil and Mohideen (1968) we know that capillaries are not uncommon on the inner surface. Capillary junctions, rather than being developed as "zonulae occludens" as in most mammals, resemble desmosomes of 0.14 μ length (Fig. 4). This may possibly be interpreted as a primitive form of capillary junction and would be worth following up further.

Sclera and cornea. The cornea consists of two major layers, which are closely connected. They are the dermal cornea, which is the modified skin covering the eye ball, and the scleral cornea, which is continuous with the cartilaginous sclera and which consists of an inner and an outer component. The dermal skin exhibits progressive corneal keratosis with increasing age and must impair vision in older specimens because of its thickness and milkiness.

Choroid and pigment epithelium. Choroid and pigment epithelium, which do not possess any obvious processes in *C. mourlani*, are conventional in their gross anatomy. Pigment cells and their uniformly-stained nuclei are relatively large. Large numbers of dark inclusions of varying sizes are present in the epithelial cells (Fig. 3). The size/frequency distribution of these objects suggests that three groups may be distinguished: tiny, globules of an average diameter of 0.17 μ; large, more or less spherical bodies of approximately 0.5 μ diameter; and ovocylindrical to cylindrical structures, about 0.5 μ in diameter and up to two microns in length. However it must be pointed out that size, abundance and distribution of granules are often linked to functional state or age of the cell, and any categorization of granules based on these parameters alone must be tentative (Fineran and Nicol, 1974). In spite of their reddish brown color in fresh specimens, all types of melanosomes are extremely electron opaque. Tapetal spheres,

---

FIGURE 3. The pigment cell layer is planar and screening pigment granules do not penetrate between outer segments (OS). Less densely-strained structures (white circles) may represent lipid bodies. The scale line is 1 μ.

FIGURE 4. A capillary within the retina with blood cells and nuclei visible. The scale line is 1 μ. The inset shows an unusual desmosome-like junction between two retinal capillaries, which may possibly be interpreted as a primitive form of capillary junction. The scale line is 0.1 μ.

which are often difficult to distinguish from spherical melanosomes, have been reported from ophidiid eyes and may also occur in *C. mourlani*. Guanine crystals, however, seem to be absent and holes in the retina, rather than being indicative of guanine material (Arnott, Best, and Nicol, 1970), are more likely to represent a reflection of the difficult fixation properties of the *C. mourlani* retina.

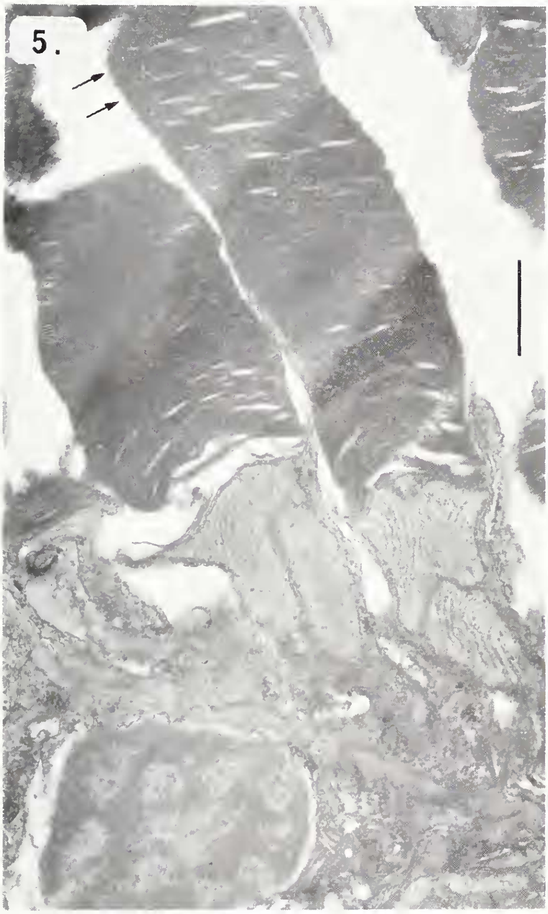
Even though lipid tapeta have been found in the eyes of ophidiids (Arnott, Maciolek and Nicol, 1970), it is doubtful whether less darkly stained circular to ovoid structures with diameters of between 1 and 2 μ represent lipid bodies, for they are not very abundant (Fig. 3) and their density is no greater in the very short inward-extending processes (Nicol *et al.,* 1975). Mitochondria, exhibiting circular or elongate (0.8×1.5 μ) profiles (indicating a cylindrical shape), were present, as well as what Fineran and Nicol (1974) term occasional "myeloids" (here: stacked membranes and smooth endoplasmic reticulum). The pigment epithelium in *C. mourlani* is planar (as in deep-sea fishes), and the pigment is likely to be stationary and confined to the cell bodies of the pigment epithelium as in other ophidiids.

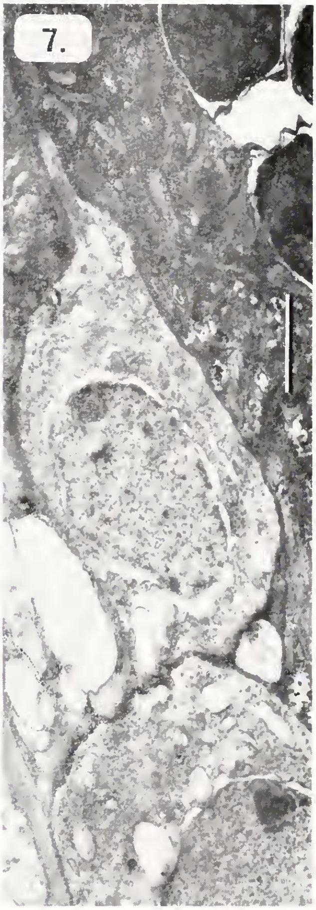
Outer segments. The outer segments of *Carapus* photoreceptor cells seem anatomically to be of one type only. Twin or double receptors as in labrid species (Fineran and Nicol, 1974) or *Scopelosaurus lepidus* (Munk, 1977), or grouped units, commonly found in the eyes of deep-sea fishes (Locket, 1970, 1971), do not occur, but a certain degree of banking with up to four tiers is observable.

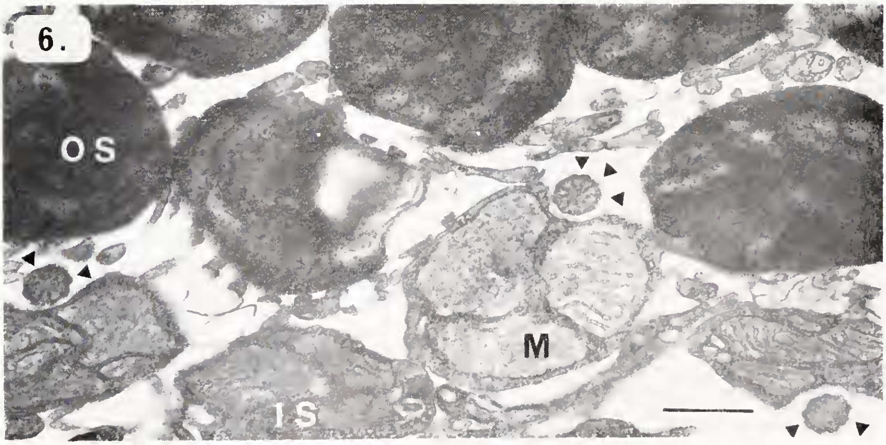
The outer segment layer is 20 μ wide, and each outer segment is approximately 5 μ long and 1 μ thick (Fig. 5). The density per 10×10 μ is 40, which corresponds to a value of 400,000 mm. Although a treatment of the retina with ZIO to distinguish unambiguously between rods and cones (Pellegrino de Iraldi, 1972) was impractical at the time, the outer segments were identified as rods using criteria recently summarized in a paper by Munk (1977). Individual rods are neither isolated from each other by envelopes of screening pigment nor are they surrounded by concentric layers of reflecting crystals (Figs. 3, 5, 6). Close contact between membranes of two or three different outer segments is, therefore, possible. Approximately 15 calycal processes, which are inner segment projections (Pietzsch-Rohrschneider, 1976), run alongside each outer segment, but do not interfere with intersegmental contact (Fig. 6). A lateral sac (Fineran and Nicol, 1974) or "accessory outer segment" (Yacob, Wise and Kunz, 1977) is not developed and obvious outer segment incisures (as in *Anableps anableps:* Borwein and Hollenberg, 1973) have not been observed with certainty. The cylindrical outer segment is made up of stacked lamellae, the spacing of which was found to be 15 nm (Fig. 5). The membranes of the lamellae are not continuous with cell membranes; they are closed and form unusually thin discs of 10 nm thickness (Fig. 5).

Inner segments. The inner segment layer is approximately 10 cells thick. Outer and inner segment, which are in direct opposition, are connected by a short cilium (Fig. 6). This shows the 9 + 0 filament arrangement typical of other visual cell cilia (Locket, 1971) and arises presumably from a centriolar body. The cilium is eccentrically placed and surrounded by a clear space, but a regular pattern in which the position of the cilium is fixed is not apparent. A second centriol was not found.

The ellipsoid is fairly short (approx. 6 μm) and possesses a cross-sectional diam-


5.


7.


6.
OS
M
IS

eter of the same order as that of the outer segment (Fig. 5). The mitochondria are largest (up to 1 μ in diameter) and most numerous at the distal end. The most sclerad-positioned mitochondria often exhibit an unusual multilamellated internal fine-structure (Schoebitz, Rodriguez-Echandia and Campos, 1973). Further vitread the mitochondria are separated from each other by fine granular cytoplasm.

The nuclei appear as mottled cylindrical organelles with rounded ends below the mitochondria. In this plane the membranes of adjacent receptor cell bodies often touch each other and may give rise to tight junctions, but whether true synapses occur is unknown.

Outer plexiform. The outer plexiform layer represents a uniform network of processes of the same dimeter (0.5 μ). These originate from a variety of cells including Muller and horizontal cells. No typical spheroids or conoids were seen, but as the fixation of this layer was poor, few valid conclusions can be drawn. Synapses do occur, but they seem atypical.

Biopolar cells and inner nuclear layer. The inner nuclear layer consists of only 1 or 2 layers of nuclei, which belong to the bipolar, amacrine, and horizontal cells. Bipolar cells are characterized by relatively large, mottled nuclei with reticulated chromatin patterns. Their plasma contains mitochondria and other normally occurring subcellular components such as ribosomes, endoplasmic reticulum, vesicles, and granules which may be glycogen (Locket, 1971).

Inner plexiform layer, ganglion cell layer and outer nerve fiber layer. The inner plexiform layer is unusually wide, and, although badly fixed, allows identification of some amacrine synapses. There are very few ganglion cells (Fig. 7) and the ratio of nuclei in the outer nuclear layer to those of the inner nuclear layer to ganglion cells is approximately 100:10:1. A similar ratio has been reported for the deep-sea fish *Coryphaenoides rupestris* by Penzlin and Friedrichsen (1973). Very few optic nerve fibers are present, but there are definitely some. The output from the retina must be small and resolution is expected to be poor.

Lens muscle. The eye of *Carapus mourlani* possesses a typical ventrally-located ectodermal lens muscle. The lens muscle, which originates from the inside of the iris close to the *ora terminalis retinae* (Munk, 1971), consists of smooth fibers.

Discussion

The eye of *Carapus mourlani* is an interesting sense organ, because it combines features of degenerated photoreceptors characteristic of cave organisms (keratosis, small number of nerve fibers, no screening pigment between the rods) with adaptations which are commonly met with in predominantly nocturnal and

Figure 5. Slightly oblique radial section through outer segment and ellipsoid portion of photoreceptor cell. The photoreceptor cells are banked, but they are of one type only. The membranes of the lamellae are not continuous with cell membranes (arrows); they are closed and form unusually thin discs. The scale line is 1 μ.

Figure 6. Transverse section through outer/inner segment junction with asymmetrically-placed connecting cilia clearly visible (arrow heads). Approximately 15 calycal processes which are inner segment (IS) projections, run alongside each outer segment (OS).

Figure 7. Section through two ganglion cells and their nuclei. The inner plexiform layer is unusually wide in the eye of *C. mourlani*, but the number of ganglion cells is very small, indicating a high degree of convergence. The scale line is 1 μ.

deep-sea forms (*e.g.*, pure rod retina, pupillary contraction, receptor-bipolar-ganglion cell ratio).

Presumably, the eye is fully functional in the larval and juvenile stages of *C. mourlani*, but degenerates with increasing age. Age-dependent retinal degenerations have been reported, for example, in the photoreceptors of the Ozark cave salamanders (Besharse and Hollyfield, 1977), and in the eye of the cave fish *Anopthichthys* (Kuhn and Kähling, 1954). The retinal structure of *Carapus* suggests that the eye of the latter is adapted to a dark environment, and that, although it must have poor resolution, it has become modified as a receptor for increased sensitivity in low environmental brightness conditions. It is believed that the visual performance of larval *Carapus* fish is better than that of adults, which spend a considerable amount of time inside holothurians, where light levels are so low that they could not be detected by sensitive light-meters (Trott, 1970).

The pupillary change, on the other hand, which can be observed in fresh specimens removed from their hosts, is direct evidence that these fish are still sensitive to different light levels. Unfortunately, it is not known at this stage whether the retinal pigment in *Carapus* migrates, at it does in many other freshwater and marine fishes (Nicol, 1965; Lang, 1965; Roeser, 1973).

Another unsolved problem concerns the formation of an image on the retina. It is generally accepted that the fish eye lens forms a good image across the full aperture due to a radial gradient of refractive index, with higher values in the center and lower ones near the periphery (for theoretical mathematical treatment see Fletcher, Murphy and Young, 1954). However, it is still an unsettled question as to whether fish eyes exhibit myopia or emmetropia (Munk, 1971; Sivak, 1976). Penzlin and Rönicke (1976) point out that, in spite of the common use of the terms "myopia", "emmetropia", and "hyperopia", these are misleading when applied to fish eyes, for one and the same eye may be both myopic and emmetropic, depending on the direction the light strikes the lens.

The lens, as in almost all fishes, is spherical in *Carapus* and cannot change its curvature. The quotient of retina-lens distance and lens radius is approximately 2 and, thus, comes close to the often cited "Mathiesen ratio" of 2.55. Ray paths and image formation, however, will have to remain speculative until more data are available on lens refractive indices.

At this stage one may, therefore, conclude that the eye of *C. mourlani* is basically a photoreceptor designed for vision in a dark environment characterized by high sensitivity and poor resolution, but that its visual performance drops with age. The age-dependent deterioration of vision is likely to be connected with the "pseudo-cave" conditions which must prevail inside the dark coelom of the fish's echinoderm host.

The authors wish to thank Dr. Leo Sosula (Prince of Wales Hospital, Randwick, N S W, Australia) for his aid in this research, and the Director of the Meat Industry Research Institute for use of the Philips EM200. Thanks are extended to Dr. Jim Chalcroft and Mr. Gary Leet for their efficient maintenance of the instrument, and the staff of the Waikato Hospital Mammography Unit for the preparation of the X-ray photograph, Figure 2 in this paper.

Summary

1. This is the first transmission electron microscope description of the retina of a parasitic fish.

2. The retina is well supplied with capillaries, some of which occur on the inner surface of the retina. An unusual and possibly primitive type of capillary junction is described.

3. The outer segments of the retina of *Carapus mourlani,* which measure approximately 2 μ in diameter, are of one type only. A certain degree of banking was observed. Outer segments are not isolated from each other by screening pigments; they are, however, surrounded by about 15 calycal processes.

4. Typical spheroids or conoids were not seen in the outer plexiform layer. The inner nuclear layer consists of only one or two layers of nuclei. The inner plexiform layer is unusually wide and some amacrine synapses can be identified. There are few ganglion cells and the ratio of nuclei in the outer nuclear layer to those of the inner nuclear layer to ganglion cells is approximately 100:10:1.

5. The eye of *C. mourlani* combines features of degenerated photoreceptors, characteristic of cave-organisms, with adaptations which are commonly found in nocturnal and deep-sea forms.

6. The visual behavior of the animal indicates that the eye is fully functional in spite of its corneal keratosis and small number of optic nerve fibers.

LITERATURE CITED

ALI, M. A., M. ANCTIL, AND H. M. MOHIDEEN, 1968. Structure rétinienne et la vascularisation intraoculaire chez quelques poissons marins de la région de Gaspé. *Can. J. Zool.*, **46**: 729–745.

ARNOLD, D. C., 1953. Observations on *Carapus acus* (Brunnick) (Jugulares, Carapidae). *Pubbl. Stn. Zool. Napoli*, **24**: 153–167.

ARNOLD, D. C., 1956. A systematic revision of the fishes of the teleost family Carapidae (Percomorphi, Blennioidea), with descriptions of two new species. *Bull. Br. Mus. (Nat. Hist.) Zool.*, **4**: 247–307.

ARNOTT, H. J., A. C. G. BEST, AND J. A. C. NICOL, 1970. Occurrence of melanosomes and of crystal sacs within the same cell in the tapetum lucidum of the stingaree. *J. Cell Biol.*, **46**: 426–427.

ARNOTT, H. J., N. J. MACIOLEK, AND J. A. C. NICOL, 1970. Retinal tapetum lucidum: a novel reflecting system in the eye of teleosts. *Science*, **169**: 478–480.

BESHARSE, J. C., AND J. G. HOLLYFIELD, 1977. Ultrastructural changes during degeneration of photoreceptors and pigment epithelium in the Ozark cave salamander. *J. Ultrastruct. Res.*, **59**: 31–43.

BORWEIN, B., AND M. J. HOLLENBERG, 1973. The photoreceptors of the "four-eyed" fish *Anableps anableps*. L. *J. Morphol.*, **140**: 405–442.

COPELAND, D. E., AND D. S. BROWN, 1976. The anatomy and fine structure of the eye in teleosts V. Vascular relations of choriocapillaris, lentiform body, and falciform process in rainbow trout (*Salmo gairdneri*). *Exp. Eye Res.*, **23**: 15–27.

COURTENAY, W. R., AND F. A. MCKITTRICK, 1970. Sound-producing mechanisms in carapid fishes, with notes on phylogenetic implications. *Mar. Biol. Berl.*, **7**: 131–137.

EMERY, C., 1880. Le specie del genere *Fierasfer* nel golfo di Napoli e regione limitrofe. *Fauna u. Flora Neapel*, **2**: 1–76.

FINERAN, B. A., AND J. A. C. NICOL, 1974. Studies on the eyes of New Zealand parrot-fishes (Labridae). *Proc. R. Soc. Lond. B. Biol. Sci.*, **186**: 217–247.

FLETCHER, A., T. T. MURPHY, AND A. YOUNG, 1954. Solutions of two optical problems. *Proc. R. Soc. Lond. A*, **223**: 216–225.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS, 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. *Bull. Am. Mus. Nat. Hist.*, **131** : 789–795.

JANGOUX, M., 1974. Sur l'"association" entre certaines asteries (echinodermes) et des poissons Carapidae. *Rev. Zool. Afr.*, **88** : 789–795.

KUHN, O., AND J. KÄHLING, 1954. Augenrückbildung und Lichtsinn bei *Anoptrichthys jordani* Hubbs und Innes. *Experientia*, **10** : 385–389.

LANG, H. J., 1965. Eine lichtmikroskopische Untersuchung der Guppy-Netzhaut. *Zeiss Mitteilungen*, **3** : 415–438.

LOCKET, N. A., 1970. Deep-sea fish retinas. *Br. Med. Bull.* **26** : 107–111.

LOCKET, N. A., 1971. Retinal anatomy in some scopelarchid deep-sea fishes. *Proc. R. Soc. London B. Biol Sci.*, **178** : 161–184.

MEYER-ROCHOW, V. B., 1972. The larval eye of the deep-sea fish *Catactyx memorabilis* (Teleostei, Ophidiidae). *Z. Morphol. Tiere*, **72** : 331–340.

MEYER-ROCHOW, V. B., 1977. Comparison between 15 *Carapus mourlani* in a single holothurian and 19 *C. mourlani* from starfish. *Copeia*, **1977** : 582–584.

MORTENSEN, T., 1923. The Danish expedition to the Kei Islands 1922. *Vidensk. Medd. Dan. Naturhist. Foren.*, **76** : 25–99.

MUNK, O., 1971. On the occurrence of two lens muscles within each eye of some teleosts. *Vidensk. Medd. Dan. Naturhist. Foren.*, **134** : 7–19.

MUNK, O., 1977. The visual cells and retinal tapetum of the foveate deep-sea fish *Scopelosaurus lepidus* (Teleostie). *Zoomorphologie*, **87** : 21–49.

NICOL, J. A. C., 1965. Migration of chorioidal tapetal pigment in the spur dog *Squalus acanthias*. *J. Mar. Biol. Assoc. U. K.*, **45** : 405–427.

NICOL, J. A. C., E. S. ZYZNAR, E. L. THURSTON, AND R. T. WANG, 1975. The tapetum lucidum in the eyes of cusk-eels (Ophidiidae). *Can. J. Zool.*, **53** : 1063–1079.

PELLEGRINO DE IRALDI, A., 1972. Differenciacion entre las cellulas fotorreceptoras (conos y bastones) rediante la reaccion con yoduro de zinc tetroxido de osmio (ZIO). *Rev. Microscopia Electronica*, **1** : 258–268.

PENZLIN, H., AND G. FRIEDRICHSEN, 1973. Die retinastruktur des Grenadier-fisches *Coryphaenoides* (*Macrurus*) *rupestris* Gunner 1765 (Macruridae, Pisces). *Zool. Anz. (Leipzig)*, **191** : 171–177.

PENZLIN, H., AND H. RÖNICKE, 1976. Zur dioptrik des Teleosteerauges-Untersuchungen am Flussbarsch (*Perca fluviatilis* Linnaeus 1758), an der Regenbogenforelle (*Salmo gairdneri* Richardson 1836) und am Goldfisch (*Carassius auratus auratus* Linnaeus 1758). *Zool. Jahrbuch Abt. Allg. Zool. Physiol. Tiere*, **80** : 413–431.

PIETZSCH-ROHRSCHNEIDER, I., 1976. Scanning electron microscopy of photoreceptor cells in the light- and dark-adapted retina of *Haplochromis burtoni* (Cichlidae, Teleostei). *Cell. Tissue Res.*, **175** : 123–130.

ROESER, K.-R., 1973. Das Auge der Fische-Feinbau und Untersuchungs-technik. *Mikrokosmos*, **62** : 208–219.

SCHOEBITZ, K., E. L. RODRIGUEZ-ECHANDIA, AND H. CAMPOS, 1973. Complex mitochondria in the retinal cones of the teleost *Galaxia platei*. *J. Microsc. (Paris)*, **18** : 109–114.

SEYMOUR, R. S., AND J. E. MCCOSKER, 1974. Oxygen consumption of the commensal fish *Carapus homei* Richardson. *Copeia*, **1974** : 971–972.

SIVAK, J. G., 1976. Optics of the eye of the "four-eyed fish" *Anableps anableps*. *Vision Res.*, **16** : 531–534.

SMITH, J. L. B., 1955. The fishes of the family Carapidae in the Western Indian Ocean. *Ann. Mag. Nat. Hist.*, **12** : 401–416.

SPRINGER, V. G., BURHANUDDIN, AND M. F. GOMON, 1974. List of fishes collected during Rumphius Expedition I. *Oseanologi di Indonesia*, **1** : 39–45.

TROTT, L. B., 1970. Contributions to the biology of carapid fishes (Paracanthopterygii: Gadiformes). *Univ. Calif. Publ. Zool.*, **89** : 1–41.

WITTENBERG, J. B., AND R. L. HAEDRICH, 1974. The choroid rete mirabile of the fish eye. II. Distribution and relation to the pseudobranch and to the swimbladder rete mirabile. *Biol. Bull.*, **145** : 137–156.

YACOB, A., C. WISE, AND Y. W. KUNZ, 1977. The accessory outer segment of rods and cones in the retina of the guppy, *Poecilia reticulata P.* (Teleostei). *Cell Tissue Res.*, **177** : 181–193.